

The Geographical Affinities of the South Pacific Island Fern Floras

G. BROWNLIE¹

ABSTRACT: The theory is proposed that the fern floras of the South Pacific, while being predominantly recently Malaysian in origin, consist also of two older elements, one being relics only of an ancient world-wide flora, the other an earlier Malaysian invasion confined now to the older and larger islands only. A fourth minor element is a recently evolved southern or subantarctic group.

MUCH HAS BEEN WRITTEN in texts on plant geography on the importance of Pacific island floras, and many papers have discussed the elements present in these floras, but these have relied largely on analyses of the phanerogams only. It is felt that the other groups of plants may yield as much information of interest, and an attempt is made here to examine the fern floras of the South Pacific from this point of view. Most of these floras are fairly well-known now, although written information for the New Hebrides is scattered, and material for the Solomons is very incomplete.

The most outstanding immediate impression is the gradual reduction in number of species from the Solomon Islands eastwards and southwards. Most of the smaller islands of course do not possess the range of habitats suitable for the establishment or development of a very diverse flora, but this general principle still applies to relatively large high islands. Copeland (1929) admits 230 species for Fiji, Christensen (1943) lists 213 for Samoa, Copeland (1932) gives 150 for the Society Islands, while New Zealand also possesses 150 species. By contrast with this, at least 300 species are known from New Caledonia with probably a much greater number in the islands to the north.

Elevation also plays a vital role in the diversity of fern floras, islands with sufficiently high mountains to develop a definite mist zone

having a very much greater number of species than low-lying islands in the same area. Wet mountain forests throughout the tropics are always the sites of the most prolific display of specific and generic variety. In Borneo, of the total of some 700 species, approximately 400 have been recorded from the single large massif of Mt. Kinabalu. An example of the difference that this factor makes is shown by a comparison of the flora of New Caledonia with that of the neighbouring low-lying Loyalty Islands. The latter possess only about 30 species—all widespread ferns or local variants of widespread species, and none of the typically New Caledonian groups are represented. This flora, which may almost be called a tropical weed fern flora, is characteristic of all low Pacific islands, the same species occurring throughout. On atolls the number of species is further reduced, but all are members of this same group.

The majority of fern genera are so widespread geographically that any attempt to distinguish relationships, evolution, and directions of distribution using this rank as a criterion becomes meaningless. This does not exclude the possibility that experimental work within any genus will not give hints as to the evolution of the genus, and of relationships both within the genus and to other genera, but most investigations of this type would need to be carried out on such a vast scale that they would occupy more than one researcher's lifetime. Consequently the pattern of specific distributions has been found the most productive in

¹Department of Botany, University of Canterbury, Christchurch, New Zealand. Manuscript received November 27, 1963.

giving any impression of the relationships existing among various Pacific island floras.

The only locally endemic genera in the area under discussion are *Loxsonia* in northern New Zealand and *Stromatopteris*, a monotypic member of the Gleicheniaceae confined to the open serpentine region in the south of New Caledonia. It is interesting that these occur in the two island groups with the longest geological history.

SAMOA AND THE SOCIETY ISLANDS

Similarities are most striking when the floras of Fiji, Samoa, and the Society Islands are compared with one another. Of the total of approximately 200 species in Samoa only 32, or 16%, are endemic, and all of these are species closely related to other local species or to ones found in Fiji. A critical comparison of the endemic species of the various Pacific islands is required because in the past there has been a marked tendency to give specific rank to any local form which varies at all from the described type, often on the basis of a single collection. This is most apparent in large and difficult genera such as *Asplenium* and *Cyclosorus*. The eight Samoan species with peculiar distribution and found nowhere else in Polynesia, as noted by Christensen (1943), are all open to misinterpretation, each apparently being based on single, possibly aberrant, individuals. Of the remaining non-endemic species, practically all are found in Fiji.

The picture presented for Samoa is repeated with minor variations in the Society Islands. Here there are approximately 150 species of ferns of which 30% are regarded as endemic. This appears to be a somewhat high figure when it is noted that Tahiti is geologically younger than Fiji with only 20% of endemics, but it may be explained on the basis of the greater elevation of the former and its greater isolation. A more likely explanation when comparing the percentage of endemics in these islands may lie in the relative propensities of the various authors to recognize local variants as true species. Again all of the Society Islands' endemics are close to other local species or to species found elsewhere in Polynesia, and Copeland (1932) admits that one, *Polypodium*

maximum (Brack.) Hook., may be an inter-specific hybrid. This aspect of hybridism which is known to occur in some fern groups in New Zealand may explain several of the rare species which appear in so many Pacific island lists on the basis of a single collection.

The remaining high island groups of southern Polynesia, the Cook Islands, Tonga, the Marquesas, and the Australs, have fern floras which are only extensions of the three major areas, Fiji, Samoa, and the Society Islands.

FIJI

Fiji represents possibly the immediate source of the fern flora of central and eastern Polynesia. Geologically it is older than these other islands and its flora is larger. However only just over 20% of this large number are endemic, and again all of these are closely related to other local species or to species on other Pacific islands, including this time the New Hebrides. Approximately 60% of the total species known in Fiji occur in these islands to the west, many extending as far as New Guinea and Indonesia. In addition to these common species, many pairs of closely related species occur in the southern islands of the New Hebrides such as *Aneityum* and Fiji. Examples of these pairs of species are *Humata botrychioides* Brack. in Fiji and *Humata multifida* (Baker) Carr. ex Brownlie in the New Hebrides, and *Orthiopteris ferulacea* (Moore) Copeland of Fiji and *Orthiopteris kingii* (Bedd.) Holtt. of the New Hebrides and farther west.

The whole effect then of the fern floras of the islands from the New Hebrides eastwards into the Pacific is that of a Malaysian group becoming gradually depleted the farther east it is traced, with probable secondary centres of diversification in the New Hebrides themselves and in Fiji.

NEW CALEDONIA

Perhaps the most interesting island from a phytogeographical viewpoint is New Caledonia. This has been realised for many years in the case of the phanerogamic flora of that island, to judge by the number of publications

on and references to the subject. An analysis of the fern flora reveals a corresponding diversity which contrasts markedly with the rather uniform Malaysian relationship of the floras of the other tropical Pacific islands. Of the approximately 300 species 127, or nearly 42%, are endemic. This is a very high proportion of plants belonging to such an old group to be confined to one island, and can only be explained on the basis of the presence of a land mass somewhere in the region for a much longer period than is the case for the other island groups discussed. Fournier (1874) postulated a greater Melanesia somewhere in this area as a source of much of the New Caledonia pteridophyte flora.

In addition to this the appearance of the flora is not so overwhelmingly that of the wet Malaysian type found in the other islands. At least a quarter of the endemic species are truly distinctive, and not merely local variant species of genera such as *Asplenium* which appear to have undergone recent evolution and speciation. The presence of several species in ancient groups like the Schizaeaceae and the Gleicheniaceae suggests relic forms from a much older period of diversification. Much interest also lies in the large number of endemic species belonging to the Lindsaeoid group of ferns. Cytological investigations on this group suggest that it possibly consists of two sections—one a fairly ancient group diversified from one another as to chromosome numbers ($n = 34, 42, 47$), and a fairly uniform group with a chromosome complement based on $n = 50$ which is typically Malaysian in distribution. It appears likely that the non-endemic species in New Caledonia belong to the latter, while the large number of taxonomically difficult local species are older forms which may not be even closely related to the widespread ones. It is also significant that most endemics of all the old groups are confined to the poorer soils of the island and to mountain ridges, while the more aggressive widespread recent Malaysian forms occupy the rain forests and the better soils.

A third element enters to a minor degree into the New Caledonian flora. This is the small group of species which are directly re-

lated to those of eastern Australia, although they are possibly indirectly also Malaysian. The various species of *Cheilanthes* would fall into this category. Some of these species occur in Malaysia but not in the humid equatorial region north of New Caledonia. Others are specifically Australian derivatives of this group.

NEW ZEALAND

The final major region in the South Pacific is New Zealand. Here the number of species is considerably less than that of New Caledonia, Fiji, or Samoa, being approximately the same as that for the most easterly sizeable group, the Society Islands. However, a comparison of the two fern floras shows major differences. Whereas the Society Islands possess no endemic genera, New Zealand has the local *Loxsonia* and an elaboration of ancient groups only surpassed in New Caledonia. A further similarity with New Caledonia is shown by the fact that the three local species of *Lindsaea* (*L. linearis* Sw., *L. trichomanoides* Dry., and *L. viridis* Col.) are cytologically distinct from one another. It seems possible that on the basis of their chromosome contents the rather isolated genera *Loxsonia* and *Leptolepia* are more nearly on the same evolutionary level, and possibly more nearly related to this old section in the Lindsaeoid group of ferns than to any other (Brownlie 1961, and unpublished).

At least one third of the New Zealand species are endemic, but here the relationships of these endemics are not with the tropical Malaysian element of the Pacific but most frequently with closely related species in eastern Australia. This relationship is so close that somewhat more than 50% of the total New Zealand fern flora is found also in the southeastern part of Australia and Tasmania (Brownlie, 1962b).

THE 'ANTARCTIC' ELEMENT

A theory which has been made much of by Copeland (1939 and 1947) is the antarctic origin of much of the world's modern fern flora. This theory was based on his belief that within different genera those showing the most primitive morphological characters were those species occurring in southern lands. The evi-

dence for this is inconclusive and may be interpreted in other ways. There is, however, within the Pacific fern floras a distinctive southern element which may in part be of recent origin. The genus *Polystichum* is a member of this group and is best developed in New Zealand and eastern Australia, but it extends northward into the Society Islands. One species is completely circum-polar and related or similar species occur in temperate South America.

Asplenium obtusatum Forst., or species very like it in both form and habitat, also occurs widely around the subantarctic extending north into eastern Polynesia. The present range in the colder parts of the Southern Hemisphere and the extreme polymorphism of this group suggests a recent origin. To this southern group probably also belong several New Zealand species of *Blechnum*, including those of the *B. procerum* complex, and some species of *Grammitis*. Only one other species, *Hymenophyllum ferrugineum* Colla, is common only to temperate South America and New Zealand. This is a much slighter relationship than could be expected if Copeland's theory of an antarctic origin were acceptable, even more so when the much-discussed similarities between the phanerogams are compared with it.

ISOLATED ISLANDS

It may be of interest to examine the floras of a number of South Pacific islands which are sufficiently isolated not to belong to any group. Pitcairn Island at the extremity of eastern Polynesia has a fern flora of only 19 species, all of which are similar to or only doubtfully distinct from those of the Society and Austral Islands (Brownlie, 1962a). This appears to be a recent flora with little or no time for local differentiation, and with none of the distinctive species of the nearest groups included. Presumably these species which have succeeded in colonising the most south-easterly extension of Polynesia are among the most successful in dispersal of the Malayan-Polynesian ferns.

Rotuma Island, an isolated volcanic cone northwest of Fiji, has a fern flora consisting of 26 species (St. John, 1954). Again, most of the species are those of wide distribution in

the tropical Pacific with one endemic, *Clycosorus rotumaensis* St. John, closely related to Fijian species, and one, *Tectaria dimorpha* St. John, whose relationships appear doubtful. This latter belongs to a group much in need of complete revision in the Malaysian-Pacific area. The most obvious similarities of the whole flora are with Fiji and the New Hebrides.

Norfolk Island, although closer to New Zealand and with many ferns in common with that country, also has several species more obviously belonging to eastern Australia. Of the total of 38 species noted by Laing (1915) only three or four are endemic, the remainder being either widespread Pacific species which occur also in Australia, or definite Australian representatives. The almost complete Australian relationship of the flora suggests long range wind dispersal as the most likely mode of arrival.

Lord Howe Island, due to its greater altitude and consequent variety of habitat, has a somewhat larger flora than Norfolk Island (Oliver, 1917) but here again the relationship is predominantly with the Australian mainland. There is, however, a suggestion of a somewhat older group shown by the endemic elaboration of the Hymenophyllaceae, a character lacking in the other isolated islands mentioned. This speciation in the *Eu-Hymenophyllum* and *Meringium* sections of the genus *Hymenophyllum* is otherwise confined to the older or larger areas, New Zealand, New Caledonia, eastern Australia, and to a minor extent Fiji. Another interesting fact is the doubtful distinction between *Asplenium pteridoides* Baker of Lord Howe and *A. polyphyleticum* Compton of New Caledonia. It seems that the fern flora of Lord Howe is not merely one with an immediate relationship to the nearest source of supply, as is the case with Pitcairn, Rotuma, and Norfolk.

DISCUSSION

The outstanding impression of the whole fern flora of the South Pacific is that it is an extension eastwards of the one found in the Malaysian area, with a gradual reduction in numbers towards the east. This is most obvious if the islands to the south of the New Hebrides are omitted. When New Caledonia and

New Zealand are included the situation appears somewhat more complex. The bulk of the flora of New Caledonia is related to that of northern islands but a not inconsiderable portion is characteristic either of that island only, or of New Zealand, eastern Australia, and New Caledonia as a unit.

It is suggested that the fern flora of this region consists of four groups:

1. An ancient group of primitive families of an old world-wide flora with a large number of its southern relics persisting in New Caledonia and New Zealand. This would include the representatives of the Osumdaceae, Schizaeaceae, and Gleicheniaceae.

2. An intermediate period flora whose relationships are somewhat obscure but which may represent an earlier Malaysian invasion of the region. Again this persists only in New Caledonia, New Zealand, and eastern Australia, and includes the Lindsaeoid endemics of New Caledonia, *Loxsonia*, *Dicksonia*, *Leptolepia*, and at least the sections *Eu-Hymenophyllum* and *Meringium* of *Hymenophyllum*.

3. A recent Malaysian section forming the bulk of the flora, and found in all areas including eastern Australia and New Zealand (where it may have arrived indirectly by wind dispersal from Australia).

4. A recently evolved southern element most conspicuous in New Zealand and eastern Australia but extending into eastern Polynesia.

The possibility remains that many of the pan-tropical and other widespread Pacific species, such as those of *Nephrolepis*, may have been aided in their distributions by human migrations in the area.

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